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Mediterranean and Atlantic deep-sea fish assemblages: differences in biomass composition and size-related structure*

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SUMMARY: Data obtained over a period of twenty years from 214 bottom trawls, towed on a single warp at depths between 402 and 1993 m in the western Mediterranean (Algerian and Balearic basins) and eastern North Atlantic (Rockall Trough and Porcupine Seabight), allowed a standardised comparison of density, biomass composition and size-related structure for both the whole fish fauna and for the most common species found within the deep-sea fish assemblages. All four areas are characterised by distinctly different and well-documented oceanographic conditions, biogeographical affinities and fishing exploitation. The results showed clear differences between the Atlantic and the Mediterranean deep-sea fish fauna, not only in density, species richness and composition, but also in the structure of the biomass that constitutes these assemblages. These differences are discussed in relation to environmental conditions and fishing pattern, which have determined the adaptive responses of both individual species and the whole ecosystem.

Key words: deep-sea, fishes, community, biomass, size, western Mediterranean, NE Atlantic.

RESUMEN: COMUNIDADES DE PECES DE PROFUNDIDAD EN EL MEDITERRÁNEO Y EL ATLÁNTICO: DIFERENCIAS EN LA COMPOSICIÓN DE LA BIOMASA Y LA ESTRUCTURA DE TAMAÑOS. – Los datos obtenidos a partir de 214 pescas de arrastre de fondo con un sólo cable, realizadas a lo largo de un período de veinte años en el Mediterráneo occidental (cuencas argelina y balear) y Atlántico nor-oriental (Rockall Trough y Porcupine Seabight), entre 402 y 1993 m de profundidad, han permitido una comparación estandarizada de la densidad y de la composición y estructura de tamaños de la biomasa, tanto del conjunto de la ictiofauna como de las principales especies comunes en estas comunidades ícticas de gran profundidad. Estas cuatro áreas se caracterizan por diferencias, ampliamente documentadas, en sus condiciones oceanográficas, afinidades bio-geográficas y de explotación pesquera. Los resultados han mostrado claras diferencias entre la ictiofauna profunda atlántica y mediterránea, no sólo en términos de densidad, riqueza específica y composición, sino también en la estructura de la biomasa que compone estas comunidades. Estas diferencias se discuten en relación con las condiciones medio-ambientales y de explotación pesquera, las cuales han determinado las respuestas adaptativas, tanto de las especies individuales como del conjunto del ecosistema.

Palabras clave: mar profundo, peces, comunidad, biomasa, tamaño, Mediterráneo occidental, Atlántico NE.

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INTRODUCTION

Estimates of biomass and abundance give an indication of the role and relative importance of populations in food webs, including the amount of energy needed for maintenance (e.g. Platt, 1985; Bergmann, 1987). A knowledge of total abundance and biomass of deep-sea fauna and how these are partitioned among different functional and size categories can be a potentially useful approach for understanding trophic relationships and energy flow into and through these ecosystems (Thurston *et al.*, 1994, Haedrich, 1996).

Furthermore, size distribution can provide information on the evolutionary responses of species and on community metabolism, and can also reflect the influence of fishing activity. However, there have been few studies of the species size and biomass spectra for deep-sea demersal fish assemblages. The only available information is from the Porcupine Seabight and the Madeira Abyssal Plain in the eastern North Atlantic (Haedrich and Merrett, 1992) and from the upper slope off southern Namibia in the southeastern North Atlantic (Macpherson and Gordoa, 1996).

In recent years, the deep-sea ichthyofauna of the Mediterranean Sea and the Atlantic Ocean has been extensively studied. In the western Mediterranean, both community structure (e.g. Stefanescu *et al.*, 1993; Moranta *et al.*, 1998) and distribution and biology of the main species have been studied (e.g. Massutí *et al.*, 1995, 1996; Morales-Nin *et al.*, 1996; Carrasón and Matallanas, 1998, 2001, 2002). In the eastern North Atlantic, there are also many publications, both on species composition and structure of assemblages (e.g. Merrett *et al.*, 1991; Koslow, 1993) and the ecology of some dominant species (e.g. Mauchline and Gordon, 1984; Gordon and Duncan, 1985; Coggan *et al.*, 1998; Allain, 2001).

From the results of the papers cited above, clear differences can be inferred between Mediterranean and Atlantic deep-sea fish assemblages. These differences are due not only to distinct species composition (e.g. Haedrich and Merrett, 1988; Stefanescu *et al.*, 1993), but also to the maximum size of individual species (Tortonese, 1960; Stefanescu *et al.*, 1992) . It is important to note, however, that misleading conclusions in comparative studies can arise from the use of different methodologies. Thus, in recent years, the importance of sampling gear when one is comparing fish assemblages has been demonstrated (e.g. Merrett *et al.*, 1991; Gordon *et al.*, 1996).

For this reason, our aim is to make a standardised comparison between biomass composition and size-related structure for both the whole fish assemblage and the most common species found in the deep sea of the western Mediterranean (Algerian and Balearic basins) and eastern North Atlantic (Rockall Trough and Porcupine Seabight). These areas are characterised by distinctly different and well-documented oceanographic conditions, surface productivity and seasonality, biogeographical affinities, biodiversity and fishing exploitation patterns.

MATERIAL AND METHODS

Study areas

The western Mediterranean is a subtropical, semi-enclosed area separated from the Atlantic by a sill in the Strait of Gibraltar, with a high degree of environmental stability for both temperature (12.8-13ºC) and salinity (38-38.6‰) below a depth of 200 m (Hopkins, 1985). The two sampled basins of the western Mediterranean (Fig. 1), the Balearic (north of the Balearic Islands) and the Algerian (south of the Balearic Islands) basins are characterised by different oceanographic and geomorphological conditions (e.g. Beckers *et al.*, 1997; Pinot *et al.*, 2002).

The Algerian basin acts as a reservoir for water of Atlantic origin. By contrast, the Balearic basin has a large cyclonic circulation, with two permanent fronts linked to the Northern Mediterranean Current and the Balearic Current (Millot, 1999). These frontal boundary regions, reinforced by the formation of a winter water mass with minimum temperature in the water column, are particularly relevant in the general oligotrophic context of the Mediterranean Sea as biologically active locations (Estrada, 1996). Moreover, the presence of numerous submarine canyons in the Balearic basin can also influence the environmental conditions in this area. These geomorphological structures play an important role in the transport and concentration of sediment to greater depths and have been proved to be areas of high productivity (Monaco *et al.*, 1990). Available estimations give the annual primary production in the northwestern Mediterranean as between 77 and 100 g C m^{-2} $year^{-1}$ (Minas *et al.*, 1988), although only about 1-5 g C m^{-2} may reach the benthic ecosystems at 800 to 1000 m depth (Miquel *et al.*, 1994).

The Rockall Trough and the Porcupine Seabight (Fig. 1) are temperate regions characterised by

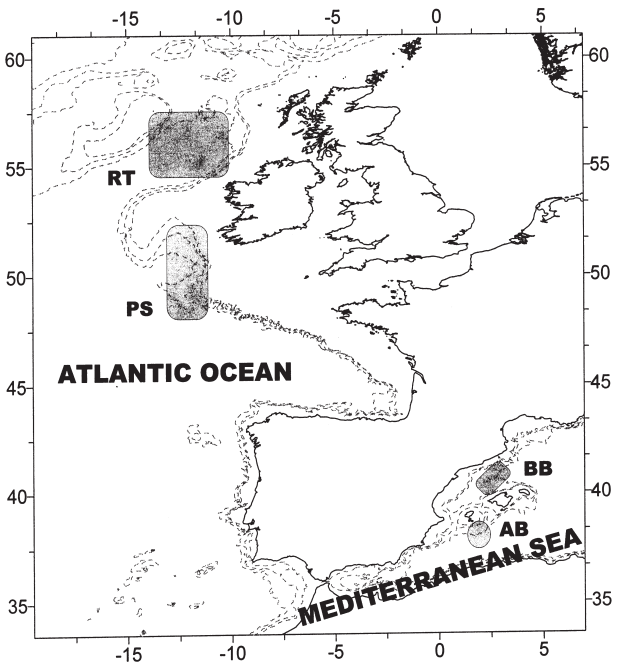

FIG. 1. – Map showing the four study areas: Balearic (BB) and Algerian (AB) basins in the western Mediterranean; and Rockall Trough (RT) and Porcupine Seabight (PS) in the eastern North Atlantic. The 500, 1000 and 2000 m isobaths are shown.

marked seasonal changes in primary productivity related to increased summer temperatures (11-14°C) in the upper water column and a seasonal thermocline. Below this, the environmental conditions are virtually constant throughout the year, with a gradual decrease in temperature with increasing depth, from about 10°C at 600 m to about 3.5ºC at 2000 m (Ellett *et al.*, 1986; Rice *et al.*, 1991). There is some evidence that the two areas could constitute a marginal oceanic region in the eastern Atlantic, where greater than average production takes place compared with adjacent regions (Mauchline, 1990). Although direct measurements of annual primary production are not available, the general rate for these areas appears to be within the range 60-100 g C $m^{-2}year^{-1}$, with a vertical flux to the deeper layers of about 12-20 g C m^{-2} (Berger *et al.*, 1989).

Sampling and data sets

Data were derived from a series of bottom trawl surveys carried out between 1978 and 1998 by different groups of researchers, studying the distribution and ecology of deep-sea benthic and benthopelagic communities. Catch data from a total of 214 hauls were used in the analysis (Fig. 2): 60 trawls between 429 and 1862 m depth (Balearic basin) and 38 trawls between 402 and 1713 m depth (Algerian basin) in the

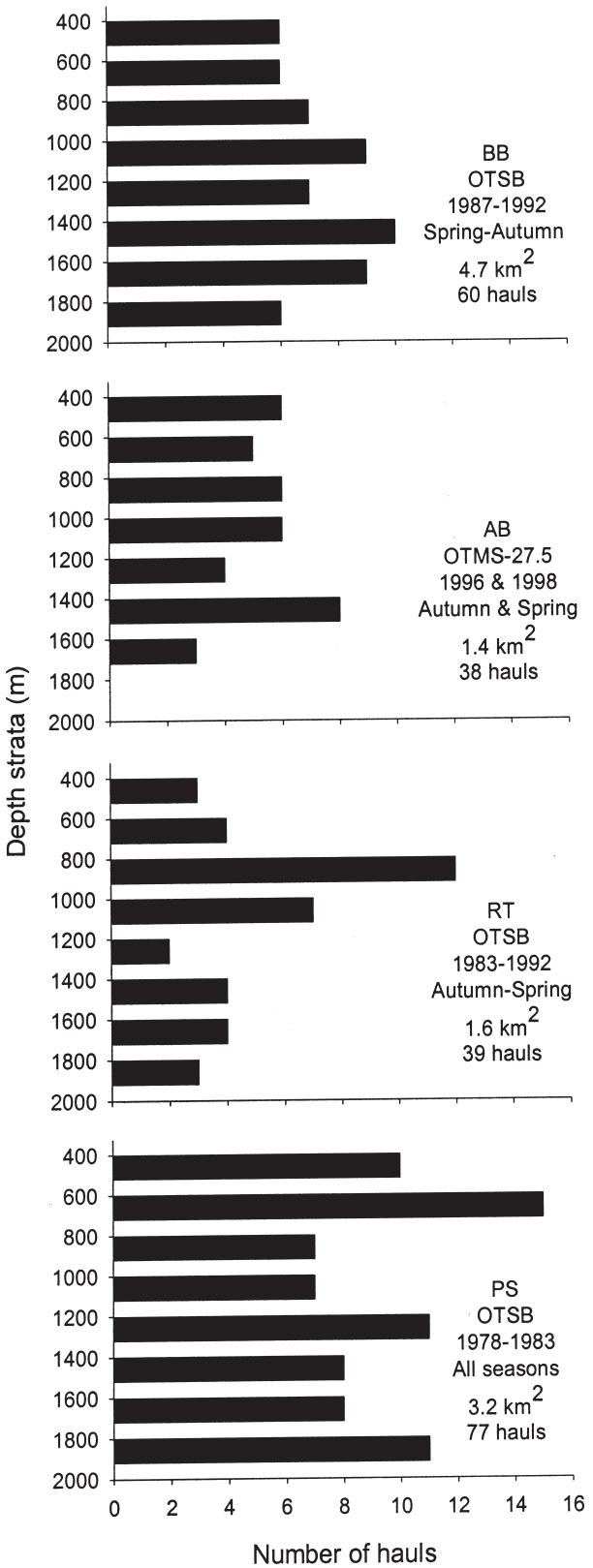

FIG. 2. – Sampling data (trawl gear used, period, area) and number of hauls (by 200 m depth-strata) used in this study for each area: Balearic (BB) and Algerian (AB) basins, in the western Mediterranean, and Rockall Trough (RT) and Porcupine Seabight (PS), in the eastern North Atlantic.

western Mediterranean; and 39 trawls between 530 and 1955 m depth (Rockall Trough) and 77 trawls between 407 and 1993 m depth (Porcupine Seabight) in the eastern North Atlantic.

As long-term routine monitoring of fish assemblages tends to be confined to the economically more important shelf species, there are relatively few long time-series of data on deep-sea fish assemblages using standardised sampling methods. For this reason, catches from different years and seasons have been pooled in our analysis.

It has also been recognised that there are considerable differences between catches, in terms of species composition, relative abundance and length frequency, from otter bottom trawls towed on single or paired warps (e.g. Merrett *et al*., 1991; Gordon *et al*., 1996). Therefore, only samples obtained by a single warp trawl were analysed. In the Rockall Trough, Porcupine Seabight and the Balearic basin, the gear used was a standard OTSB-14 (e.g. Rucabado *et al*., 1991), whereas in the Algerian basin the modified semi-balloon otter trawl OTMS-27.5 (Sardà *et al*., 1998) was used. Both gears were towed at 2.5 knots and had similar vertical openings (1.5-2.0 m), with their effective horizontal openings considered to be around 6.7 and 14 m respectively and a codend mesh size of 12 mm.

Values were obtained for the number and weight of individuals, as well as the length frequencies of demersal fish species at each station. Depending on the morphology of the species examined, total length, head length, pre-anal length, standard length or gnathoproctal length was measured for the total catch or for random sub-samples. Biomass and abundance were standardised to a common sampled area (1000 m^2), according to the methodology most commonly employed in studies of deep-sea fish assemblages. This calculation takes into account the greater path width of the OTMS - 27.5 trawl. This trawl was specifically designed to improve the catch rates of decapod crustaceans, but it also yielded some significantly different catch rates of some fish species (Sardà *et al.,* 1998). Weight was calculated using available length-weight relationships obtained during these samplings.

Data analysis

For analysis, the data were grouped into the following depth intervals: 400-800 m, 800-1400 m and 1400-2000 m. These depth strata approximately correspond to the upper, middle and lower slopes proposed by Haedrich and Merrett (1988) in the North Atlantic, and to the different fish groups identified along the continental slope of the western Mediterranean (Stefanescu *et al.,* 1993; Moranta *et al*., 1998).

Standardised catch data were pooled for these depth intervals, and the ecological parameters of species richness, biomass (kg 1000 m^{-2}) and abundance (n.1000m^{-2}) were determined. For comparative purposes, the geometric mean [ln (x+1)] was preferred to the arithmetic mean for biomass and abundance, in order to minimise the negative effect of extreme values. The normality of these parameters was examined for standard skewness and kurtosis, and the homogeneity of variance was investigated using Cochran's test. The examination of the data, with unbalanced numbers of hauls per region and depth strata, indicated that the assumptions of normality and homogeneity of variances were violated. However, according to Underwood (1997), the analysis of variance may be considered robust and not greatly affected by violations of the assumptions where samples are relatively large ($n > 6$) and a more conservative significance level is adopted (in this case $p < 0.01$). Two-factor orthogonal analysis of variance (ANOVA) was used to test differences between the mean values of the ecological parameters for both studied areas and depth strata. After ANOVA, a Bonferroni multiple range test was applied to determine which means were significantly different.

Cluster analyses using the Bray-Curtis index and the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) as the aggregation algorithm was applied to calculate and visualise similarities between the taxonomic composition, both in terms of biomass and abundance of main groups, by depth strata and area. For the analysis, only the groups representing more than 0.1% of the total catch in the assemblage were considered. The Bray-Curtis index was also applied to calculate the similarity percentage between areas in terms of species composition.

Biomass by size class for each assemblage was estimated following standard methodologies, using $\log_2$ groupings of fish weight (g) on the *x*-axis (e.g. Macpherson and Gordoa, 1996). Correspondence analysis was used to examine the patterns of variation of assemblages in relation to different size classes. This technique has the advantage of providing a simultaneous representation of variables (assemblages) and descriptors (size classes) in a common system of orthogonal axes.

TABLE 1. – Mean standardised biomass and abundance for each assemblage (± standard error) and results of the statistical analysis (BB, Balearic basin; AB, Algerian basin; RT, Rockall Trough; PS, Porcupine Seabight; US, upper slope; MS, middle slope; LS, lower slope; SS, sum of squares; DF, degrees of freedom; F, statistic). *, indicate P < 0.01.

	Mediterranean Sea					
	Balearic Basin			Algerian Basin		
	Upper	Middle	Lower	Upper	Middle	Lower
kg 1000 m^{-2}	0.16±0.01	0.42±0.05	0.12±0.01	0.15±0.03	0.81±0.05	0.44±0.06
n.1000 m^{-2}	6.53±0.42	3.52±0.32	3.44±0.35	3.74±0.73	3.48±0.22	3.74±0.42
	Atlantic Ocean					
	Rockall Trough			Porcupine Seabight		
	Upper	Middle	Lower	Upper	Middle	Lower
kg 1000 m^{-2}	4.16±1.34	4.36±0.51	3.02±0.81	0.93±1.42	1.23±0.11	1.02±0.13
n.1000 m^{-2}	18.22±4.61	24.97±2.93	12.91±3.34	16.92±2.52	10.15±1.10	7.02±1.13

a) Statistical test for biomass ln (x+1) transformed

Analysis of variance	SS	DF	MS	F
Area	34.44	3	11.48	135.4*
Depth	2.22	2	1.11	13.07*
R x D	0.84	6	0.14	1.66
Residual	17.14	202	0.08	
Total	62.14	213		

Bonferroni test

Area				
Group	BB (1)	AB (2)	RT (3)	PS (4)
Mean	0.18	0.35	1.43	0.64
Differences	$^{1-2}$0.17	$^{2-3}$1.09*	$^{3-4}$0.80*	
	$^{1-3}$1.26*	$^{2-4}$0.29*		
	$^{1-4}$0.46*			
Depth				
Group	US (1)	MS (2)	LS (3)	
Mean	0.58	0.80	0.58	
Differences	$^{1-2}$-0.22*	$^{2-3}$0.22*		
	$^{1-3}$-0.00			

b) Statistical test for abundance ln (x+1) transformed

Analysis of variance	SS	DF	MS	F
Area	43.61	3	14.54	44.82*
Depth	3.61	2	1.83	5.64*
R x D	4.96	6	0.83	2.55
Residual	65.52	202	0.33	
Total	134.66	213		

Bonferroni test

Area				
Group	BB (1)	AB (2)	RT (3)	PS (4)
Mean	1.59	1.48	2.79	2.26
Differences	$^{1-2}$-0.11	$^{2-3}$1.30*	$^{3-4}$0.53*	
	$^{1-3}$1.19*	$^{2-4}$0.78*		
	$^{1-4}$0.67*			
Depth				
Group	US (1)	MS (2)	LS (3)	
Mean	2.19	2.06	1.83	
Differences	$^{3-1}$0.36*	$^{3-2}$0.23		
	$^{2-1}$0.13			

RESULTS

Biomass and abundance

The samples analysed yielded a total biomass of 11153 kg belonging to 140 species of 46 families (Appendix). Despite the different sampling effort in each area, large differences between the Mediterranean and the Atlantic assemblages were observed in the total catch. The 1.4 and 1.6 km^2 sampled in the Algerian basin and the Rockall Trough respectively yielded a total catch of 719 and 6089 kg respectively. Similarly, in the Balearic basin (4.7 km^2 sampled) and the Porcupine Seabight (3.2 km^2 sampled), the total catch was 976 and 3369 kg respectively.

No interactions were identified between the variables area and depth strata, and standardised biomass and abundance values were found to be significantly different for both of these variables. The highest values were from the Rockall Trough and the lowest values were from the two Mediterranean areas. There was no significant difference between biomass and abundance values for the two Mediterranean areas (Table 1). There were significant differences in biomass between depth strata due to the high biomass values of middle slope assemblages, whereas for abundance the only significant difference was between the upper and lower slope.

Species richness and taxonomic composition

The number of species captured was 43 in the Balearic basin, 47 in the Algerian basin, 80 in the Rockall Trough and 104 in the Porcupine Seabight (Table 2). The percentage similarities within both the Mediterranean and Atlantic areas were much

TABLE 2. – Total number of species (in bold) in each studied area and common species and percentage similarity (from Bray-Curtis similarity index) between the areas: Balearic basin (BB); Algerian basin (AB); Rockall Trough (RT); Porcupine Seabight (PS).

	Percentage similarity			
	BB	AB	RT	PS
BB	**43**	85	35	38
AB	35	**47**	34	35
RT	23	22	**80**	75
PS	27	26	69	**104**
	Number of common species			

higher than between the Mediterranean and Atlantic assemblages. A similar trend was evident when the number of species in common between areas was examined (Table 2).

In the Mediterranean, there was no obviously predominant family over the whole depth range (Table 3). The dominant families of the upper slope assemblages were Gadidae and Scyliorhinidae in terms of biomass and Gadidae and Macrouridae in terms of abundance. On the middle slope, Moridae and Alepocephalidae dominated in terms of biomass, while Moridae, Alepocephalidae and Macrouridae dominated in terms of abundance. On the lower slope, Alepocephalidae was the most important family in terms of biomass, whereas Chlorophthalmidae and Macrouridae dominated in terms of abundance.

By contrast, in both the Atlantic areas, the family Macrouridae was the most important in terms of biomass throughout the whole depth range surveyed (Table 3), although other important families included Gadidae and Chimaeridae on the upper slope, Moridae and Alepocephalidae on the middle slope and Synaphobranchidae on the lower slope. Synaphobranchidae and Macrouridae were the most important families in terms of abundance at all depth strata.

TABLE 3. – Percentage biomass and abundance (between brackets) composition for the most important families obtained by depth-strata in each area.

Upper	%		Middle	%		Lower	%	
BALEARIC BASIN								
Gadidae	42.3	(46)	Moridae	39.3	(59)	Alepocephalidae	36.4	(5)
Scyliorhinidae	22.9	(2)	Alepocephalidae	15.0	(8)	Chlorophthalmidae	23.1	(51)
Macrouridae	20.5	(24)	Macrouridae	13.8	(12)	Moridae	20.7	(11)
Moridae	6.0	(5)	Gadidae	11.6	(2)	Squalidae	7.9	(0.7)
Notacanthidae	2.5	(4)	Hexanchidae	6.3	(0.1)	Macrouridae	7.7	(24)
Squalidae	1.8	(1)	Squalidae	3.8	(0.3)	Bythytidae	1.8	(3)
Cynoglossidae	1.3	(7)	Scyliorhinidae	3.6	(1)	Scyliorhinidae	1.2	(0.1)
			Lophiidae	3.3	(0.1)	Notacanthidae	1.1	(5)
ALGERIAN BASIN								
Gadidae	41.7	(43)	Moridae	35.5	(17)	Alepocephalidae	74.5	(22)
Scyliorhinidae	28.6	(13)	Alepocephalidae	32.5	(33)	Squalidae	10.0	(3)
Macrouridae	11.0	(23)	Scyliorhinidae	12.1	(7)	Moridae	6.8	(4)
Trachichthyidae	6.2	(5)	Squalidae	5.4	(2)	Scyliorhinidae	3.0	(0.6)
Squalidae	5.8	(3)	Gadidae	4.7	(5)	Chlorophthalmidae	2.7	(47)
Trichiuridae	1.0	(0.9)	Macrouridae	4.0	(29)	Macrouridae	2.1	(21)
ROCKALL TROUGH								
Macrouridae	43.1	(22)	Macrouridae	38.0	(37)	Macrouridae	62.7	(8)
Chimaeridae	18.1	(5)	Alepocephalidae	16.9	(5)	Synaphobranchidae	10.9	(33)
Gadidae	13.0	(3)	Squalidae	11.6	(1)	Moridae	8.7	(4)
Squalidae	7.0	(0.3)	Gadidae	9.0	(0.5)	Chimaeridae	4.0	(0.4)
Moridae	7.0	(21)	Moridae	6.8	(6)	Alepocephalidae	3.9	(1)
Trichiuridae	2.2	(0.3)	Chimaeridae	6.3	(5)	Squalidae	3.4	(0.5)
Synaphobranchidae	1.3	(40)	Synaphobranchidae	3.9	(39)			
			Rajidae	2.3	(0.1)			
PORCUPINE SEABIGHT								
Macrouridae	19.1	(21)	Macrouridae	33.0	(30)	Macrouridae	39.3	(24)
Gadidae	16.7	(6)	Moridae	29.0	(13)	Synaphobranchidae	20.6	(59)
Moridae	14.9	(18)	Trachichthyidae	9.8	(2)	Alepocephalidae	8.9	(4)
Lophiidae	13.4	(0.1)	Alepocephalidae	8.8	(2)	Moridae	7.9	(4)
Squalidae	9.7	(0.3)	Squalidae	4.7	(0.1)	Trachichthyidae	5.7	(2)
Trachichthyidae	7.2	(2)	Rajidae	4.1	(0.1)	Squalidae	5.4	(0.2)
Chimaeridae	6.1	(0.6)	Synaphobranchidae	3.1	(47)	Bythytidae	2.5	(0.2)
Scorpaenidae	3.5	(0.7)	Scorpaenidae	2.3	(0.3)	Chimaeridae	2.4	(0.4)
Synaphobranchidae	2.8	(46)	Chimaeridae	1.1	(0.6)	Notacanthidae	1.4	(4)
Alepocephalidae	1.7	(0.5)	Gadidae	1.1	(0.2)	Ophidiidae	1.3	(0.3)
Notacanthidae	1.1	(1.7)						

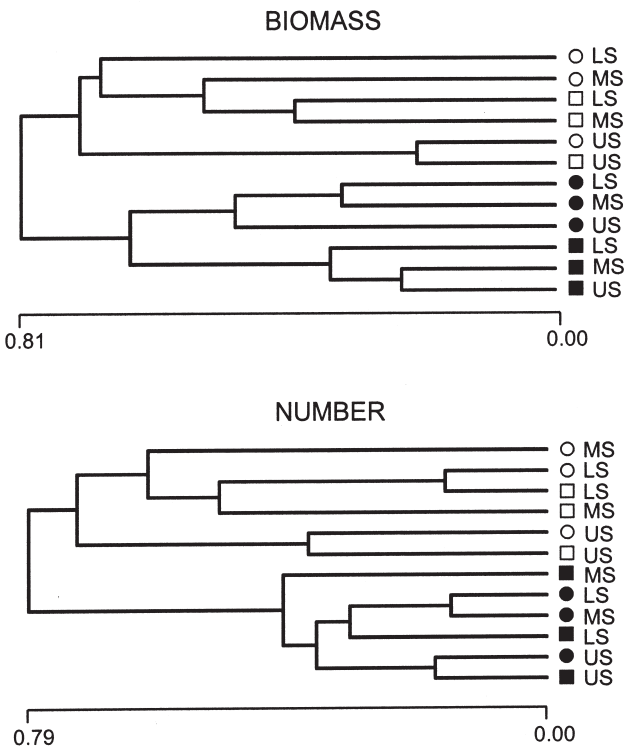

FIG. 3. – Similarity dendrograms of catch composition of total assemblages by area (○, Balearic basin; ❑, Algerian basin; ■, Rockall Trough; ●, Porcupine Seabight) and depth-strata (US, Upper slope; MS, Middle slope; LS, Lower slope), in terms of standardised biomass (kg 1000 m^{-2}) and abundance (n. 1000 m^{-2}), for the main taxonomic groups in each assemblage (see Table 3).

The dendrograms derived from the standardised values of biomass and abundance for taxonomic groups showed clear differentiation, in the first cluster, between Mediterranean and Atlantic assemblages (Fig. 3). The second cluster in the Mediterranean assemblage separated the upper from the middle and lower slope, both in terms of biomass and abundance, while in the Atlantic this bathymetric segregation was not so clear and the second dichotomy separated the Rockall Trough and the Porcupine Seabight assemblages in terms of biomass, but not abundance.

Size-related structure

The biomass spectra for the whole depth range surveyed in each area (Fig. 4) showed a clear gradient from the Balearic basin, in which 88% of the biomass was found between size classes 3 and 9 with a mode at 7, to the Rockall Trough, in which 80% of the biomass was situated between size classes 8 and 13, with a mode at 10. The Algerian basin and the Porcupine Seabight had intermediate modes,

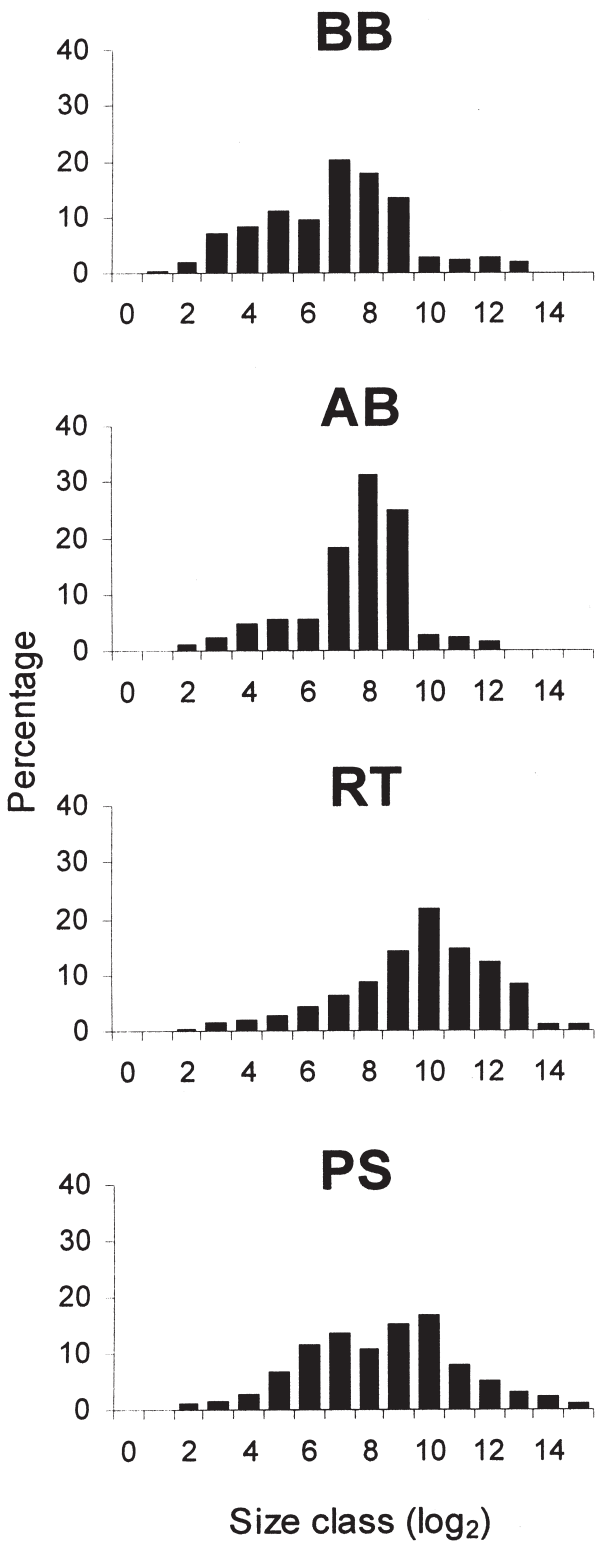

FIG. 4. – Percentage of total biomass by size-class in the four studied areas: Balearic (BB) and Algerian (AB) basins, in the western Mediterranean; and Rockall Trough (RT) and Porcupine Seabight (PS), in the eastern North Atlantic.

with more than 85% of the biomass from size classes 4-9 and 5-12 respectively.

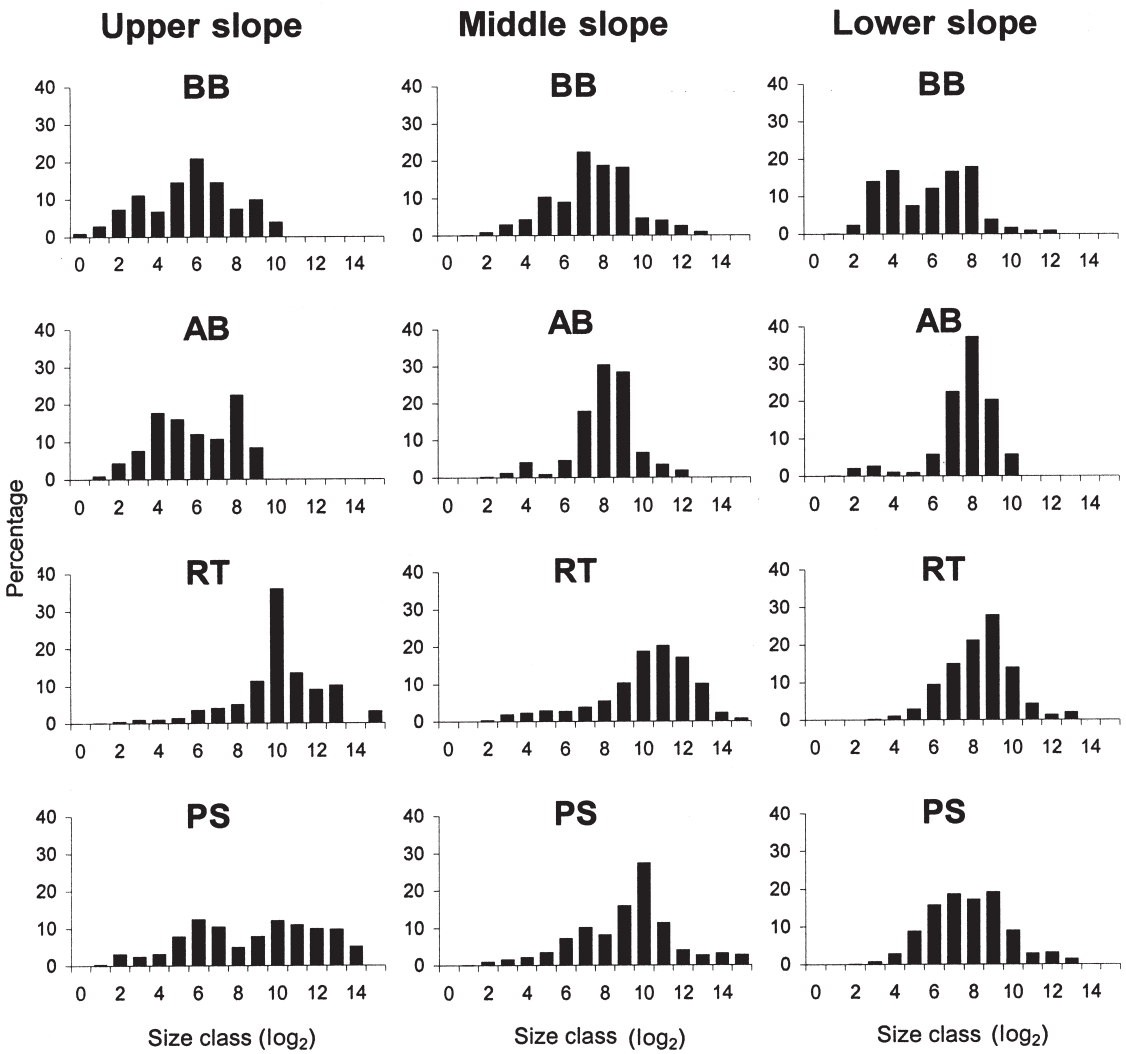

FIG. 5. – Percentage of total biomass by size-class and depth-strata in the four studied areas: Balearic (BB) and Algerian (AB) basins, in the western Mediterranean; and Rockall Trough (RT) and Porcupine Seabight (PS), in the eastern North Atlantic.

Similar trends were observed for the selected depth strata (Fig. 5), with greater differences on the upper slope, where a higher percentage of the biomass was comprised of size classes ≤ 6 in the Mediterranean assemblages and of size classes ≥ 5 in the Atlantic assemblages. The only exception was found on the lower slope, where the biomass spectrum from the Algerian basin was similar to those found in the Atlantic assemblages. The correspondence analysis applied to biomass spectra by depth strata showed that data were arranged in a parabolic form (Fig. 6), which signified a clear gradient. The first axis (F1) explained 58% of the variability and discriminated between the Mediterranean assemblages, in which biomass was mainly distributed in small and middle size classes, and the Atlantic assemblages, which were more related to larger size classes (10-13).

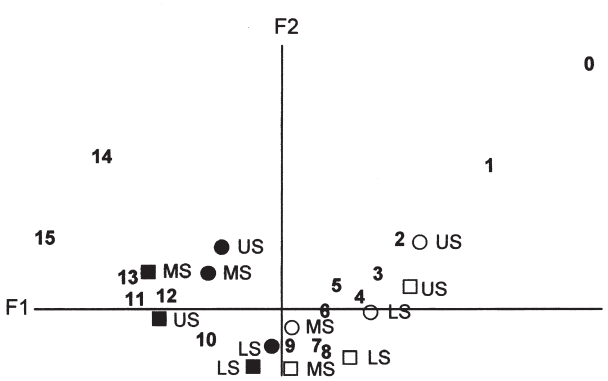

FIG. 6. – Correspondence analysis of biomass spectra of total assemblages by area (○, Balearic basin; ❑, Algerian basin; ■, Rockall Trough; ●, Porcupine Seabight) and depth-strata (US, Upper slope; MS, Middle slope; LS, Lower slope). Numbers correspond to the size classes of Figure 5.

TABLE 4. – Average (arithmetic Mean), minimum (Min) and maximum (Max) length (TL, total length; GL, gnathoproctal length; HL, head length) of the species appearing in the four assemblages (BB, Balearic basin; AB, Algerian basin; RT, Rockall Trough; PS, Porcupine Seabight), in which more than ten specimens could be measured (n).

Area	Mean	Min	Max	n	Area	Mean	Min	Max	n
Centroscymnus coelolepis cm TL					*Coelorhynchus coelorhynchus* cm HL				
BB	27.4	17	61	46	BB	4.5	1.6	7.9	75
AB	36.9	20	91	39	AB	3.6	3.1	4.3	27
RT	96.4	84	112	54	RT	6.6	2.9	9.5	119
PS	92.2	78	106	13	PS	5.8	1.7	8.5	58
Notacanthus bonapartei cm GL					*Nezumia aequalis* cm HL				
BB	4.7	3.9	9.5	88	BB	2.7	0.9	4.6	575
AB	4.2	2.5	10.0	25	AB	3.5	0.9	4.6	1871
RT	8.9	4.0	22.0	649	RT	3.9	1.1	6.0	2878
PS	10.0	3.0	27.0	346	PS	3.4	1.7	8.5	4006
Polyacanthonotus rissoanus cm GL					*Coelorhynchus labiatus* cm HL				
BB	5.1	3.5	6.0	71	BB	4.8	1.9	6.3	118
AB	5.5	3.5	6.0	28	AB	4.6	1.9	6.6	162
RT	9.1	4.0	20.0	275	RT	6.1	2.9	11.3	1140
PS	10.5	4.0	19.0	528	PS	5.6	1.7	11.0	415
Phycis blennoides cm TL					*Coryphaenoides mediterraneus* cm HL				
BB	14.5	6.0	62.0	1282	BB	3.2	1.7	4.2	84
AB	16.7	6.0	53.0	540	AB	2.3	0.7	3.8	202
RT	34.8	10.1	68.2	130	RT	5.0	1.8	13.2	317
PS	27.4	6.8	71.6	284	PS	5.0	1.4	16.5	408
Mora moro cm TL					*Helicolenus dactylopterus* cm TL				
BB	31.5	5.0	50.0	329	BB	12.5	3.0	32.0	205
AB	34.8	11.0	53.0	324	AB	9.7	2.0	29.0	562
RT	39.9	17.2	72.7	83	RT	17.1	11.4	24.7	40
PS	44.2	6.1	72.7	193	PS	20.6	6.6	38.0	89

Clear size differences were also observed, at a species level, by comparing the length of ten species captured in significant numbers within the four areas (Table 4). In all cases, both maximum (with the only exception of *Helicolenus dactylopterus*) and mean lengths were higher in the Atlantic than in the Mediterranean. By contrast, minimum lengths were more similar, with the only exceptions of *Centroscymnus coelolepis* and *Helicolenus dactylopterus*, where the minimum size in the Atlantic was at least double that found in the Mediterranean.

DISCUSSION

The standardised comparisons of this study confirm the clear differences between the deep-sea demersal fish fauna of the Mediterranean and the Atlantic, which were already suggested four decades ago by Tortonese (1960) and more recently shown, at a species level, by Stefanescu *et al.* (1992) and D'Onghia *et al.* (1998).

Biomass and abundance

The biomass and abundance indices were lower for the Mediterranean assemblages than for the Atlantic. The factors that cause these differences are likely to be complex. Although the influence of surface productivity on demersal megafauna is poorly understood, pelagic production and its arrival, as phytodetritus, on the sea floor has been reported as one of the most important sources of organic matter for the northwestern Mediterranean (Miquel *et al.*, 1994) and eastern North Atlantic (Rice *et al.*, 1986) deep-sea ecosystems. Although similar ranges of surface productivity have been estimated in these areas, the availability of organic matter at the seabed in the Atlantic, which has been estimated as an order of magnitude higher than in the Mediterranean (around 20% and 2-5%, respectively; see Material and Methods), could contribute to the differences in density of fish fauna between the two areas. The higher temperature below 200 m in the Mediterranean could contribute to a faster decompo-

sition of the organic matter during its transport through the water column before its arrival to the sea floor as food source.

Studies on the diets of deep-water fishes in the Rockall Trough (Mauchline and Gordon, 1991 and references cited therein) have shown the dominance of meso, bathy and benthopelagic prey. Therefore, the enhanced demersal biomass down to about 1000-1500 m depth most probably results from the efficient transfer of surface production, via overlapping food chains and vertical migration of prey. Conversely, in the western Mediterranean, it has been suggested that this energy transfer mechanism only reaches about 800-1000 m depth (Cartes, 1998).

The higher values of fish abundance obtained from the upper slope of the Balearic basin could be related to the presence of submarine canyons, which were absent in the Algerian basin. It has been shown that these geomorphological structures are a means of transporting sediments rich in organic matter from the continental shelf, and that they also create a focus for diel migrations of plankton from upper levels (Macquart-Moulin and Patriti, 1993). These canyons can act as recruiting grounds for both fish (Stefanescu *et al*., 1994) and crustaceans (Cartes *et al*., 1994). Similarly, the Rockall Trough has a gentle slope, with no canyons, and except at around 400-500 m, is composed of soft mud with an increasing biogenic content with depth (Mitchell *et al*., 1997), while the Porcupine Seabight is bisected by canyons (Rice *et al*., 1991) that separate a northern and a southern trawlable area. The northern area is comprised of very soft sediments, especially at mid-slope depths, and dense aggregations of the sponge, *Pheronema carpenteri* (Rice and Thurston, 1990). Multivariate analysis separated the catches of the larger paired warp trawl between these two areas, but the OTSB catches were not separable (Gordon *et al*., 1996).

The biomass indices showed some similar bathymetric trends between all four areas, with a maximum on the middle slope, while abundance indices were more variable. The peak of biomass in both the Balearic and Algerian basins occurs at between 1000 and 1200 m depth (Stefanescu *et al*., 1993; Moranta *et al*., 1998 respectively), which results both from some medium and large-sized species reaching their greatest abundance at these depths (e.g. *Alepocephalus rostratus*, Morales-Nin *et al*., 1996) and from other species reaching their greatest biomass due to a bigger deeper trend (e.g. *Trachyrincus scabrus* and *Phycis blennoides*; Massutí *et al*., 1995 and 1996 respectively). The isobath of 1200 m is considered to be about the lower limit of the mesopelagic fauna and the reduction of this trophic resource probably accounts for the decline in biomass on the Mediterranean lower slope (Stefanescu *et al*., 1993). In the Rockall Trough, biomass had maximum values at mid-slope depths. This peak, which was evident using several different trawls (Gordon, 1986), is most probably related to the depth range of greatest potential vertical and horizontal impingement of epi- and mesopelagic fauna on the slope (Mauchline and Gordon, 1991). Similar results were obtained using several trawl types in the Porcupine Seabight (Merrett *et al*., 1991).

Species richness and taxonomic composition

Atlantic assemblages are composed of a larger number of species than those of the Mediterranean, which has been widely described as being less diverse than the Atlantic for some groups (Bouchet and Taviani, 1992). The more constant physical environment and the recent origin of the deep-sea fauna of the Mediterranean (Pérès, 1985) probably accounts for the fewer number of species. In the Atlantic, the Porcupine Seabight has a greater number of species than the Rockall Trough. The Rockall Trough is a semi-enclosed area, which is only open to the deeper water in the south. The relatively shallow sills to the west and north create a physical barrier to the movement of deep-water fish species. The markedly different hydrographic differences between the Rockall Trough and the Norwegian Sea have resulted in almost no similarity in the deep-water fish fauna between these areas (Bergstad *et al*., 1999). On the other hand, there are many species in common between the Rockall Trough and the Porcupine Seabight (Gordon *et al*., 1996). The Porcupine Seabight also has affinities with the northwest African slope, where there is a high diversity in some families (e.g. Alepocephalidae; Merrett and Domanski, 1985), and the presence of some species has been attributed to the presence of a Lusitanian (Mediterranean) influence in the area (e.g. *Hoplostethus mediterraneus*; Ratz, 1984). Mediterranean water is clearly identified in the Porcupine Seabight (Rice *et al*., 1991), but previous reports of traces of Mediterranean water in the Rockall Trough are now being questioned (New and Smythe-Wright, 2001). In addition to these biogeographic factors, the proximity of the slope of the Porcupine Seabight to abyssal depths compared to that of the Rockall Trough could also increase the

species number in this area, through the capture of juveniles of abyssal-living species (e.g. *Coryphaenoides leptolepis* and *Coryphaenoides carapinus*).

There are some very clear differences in the families that dominate the biomass between the Mediterranean and the Atlantic. In the Mediterranean, a different family dominates each of the bathymetric zones: Gadidae on the upper slope, Moridae on the middle slope and Alepocephalidae on the lower slope. By contrast, in the Atlantic the family Macrouridae was dominant in each bathymetric zone. The different food availability and the partitioning of the main trophic resources within these ecosystems (among mostly fish in the Atlantic and between decapods and fish in the Mediterranean) may explain some of these differences. The dominant Macrouridae in the Atlantic (*Coryphaenoides rupestris*, *Nezumia aequalis* and *Coryphaenoides guentheri*) feed on small macroplankton (Mauchline and Gordon, 1984). On the upper and middle slope of the Mediterranean, this trophic resource may also be used by benthopelagic decapods, which in turn could provide food for the dominant fish and/or for their prey [Gadidae, Scyliorhinidae, Macrouridae and Moridae (Macpherson, 1978, 1980; Carrasón *et al*., 1997, Carrasón and Matallanas, 2002)]. The Alepocephalidae are dominant on the Mediterranean lower slope. They have a conservative feeding strategy (float and wait), typical of oligotrophic conditions (Haedrich, 1996), which seems to confer an advantage over the more active foragers (Macrouridae and Synaphobranchidae) that predominate on the Atlantic lower slope.

Size-related structure

Biomass spectra show the distribution of overall biomass within the assemblages and can indicate the relative importance of different fish sizes with respect to energy flow (Haedrich and Merrett, 1992). According to these authors, flat spectra correspond to areas where food supply is rather uniform over the entire year, whereas spiky spectra characterise areas where production is pulsed. The observed patterns in the Mediterranean and the Atlantic both show a predominantly modal biomass spectrum, suggesting that their most important energy source might be seasonal.

The biomass spectra show clear differences between Mediterranean and Atlantic assemblages where, respectively, small-middle and middle-large size classes predominate. Where the same species occurs in both the Mediterranean and the Atlantic, those in the Mediterranean tend to attain a smaller adult size. As a consequence, these fish will have smaller mouths and will therefore utilise a different component of the available food resource. Competition for this food resource by the invertebrate fauna, notably the decapod crustaceans, may be an important factor in determining the overall biomass spectra (Cartes *et al*., 2001).

The differences in biomass spectra between Mediterranean and Atlantic assemblages depend on the depth strata. Differences were greatest on the upper slope and these are most likely related to the fishing exploitation of this bathymetric range in both Mediterranean areas, where important bottom trawl fisheries targeting decapod crustaceans have been carried out since the 1960s (Bas *et al*., 1985). Fishing exploitation has been demonstrated as an important factor affecting distribution of biomass within benthic fish assemblages (Macpherson and Gordoa, 1996). On the unexploited lower slope, biomass spectra were similar in the Atlantic assemblages. However, some differences could be observed in the Mediterranean, where the distribution was skewed to small-sized classes compared to the Atlantic. In the Balearic basin, there were two evident modes at small and middle-size classes, while in the Algerian basin there was a main mode at the middle-size class. Differences between the deep-sea fauna of these two western Mediterranean basins have been reported previously, not only in fish fauna (Moranta *et al*., 1998), but also in bathyal decapod crustaceans (Maynou and Cartes, 2000). These differences have been attributed to the fact that trophic webs in the Algerian basin depend more directly on food of planktonic origin, while in the Balearic basin, where there are important submarine canyons, benthic prey enhances food availability and allows a broader trophic spectrum. Thus, the greater percentage of biomass on the lower slope of the Algerian basin corresponds to the middle-sized species *Alepocephalus rostratus* (almost 75%), whose diet is based on gelatinous macroplankton (Carrasón and Matallanas, 1998), while in the Balearic basin its importance decreases (representing 36%) and other small-sized species such as *Bathypterois mediterraneus* and *Lepidion lepidion*, which prey upon benthopelagic crustaceans (Carrasón and Matallanas, 2001) and benthic decapods (Carrasón *et al*., 1997) respectively, also represent an important fraction of the biomass (23

and 21% respectively). The greatest similarities between Mediterranean and Atlantic deep-sea fish assemblages were found on the middle slope. This might be due to the similar trophic webs present in this bathymetric range, in which a great proportion of the biomass (> 60%) corresponds to the macronekton foragers and/or epibenthos predators (Macrouridae and Moridae) and to the macroplanktonivores (Alepocephalidae).

The differences in the biomass structure between Mediterranean and Atlantic assemblages were also evident at a species level, when both mean and maximum lengths of species caught in all surveyed areas were compared. The small size of Mediterranean deep-sea fishes has already been discussed by Tortonese (1960) and more recently by Stefanescu *et al*. (1992). According to these authors, it is evident that this phenomenon is very complicated and is undoubtedly the result of a combination of factors of disparate origin (e.g. latitudinal gradients on fish size, ecological factors affecting body size). More limited resources and a high temperature in the Mediterranean (~ 13ºC compared to 10 to 4ºC in the eastern Atlantic areas) could also be assumed to play an important part.

In summary, the differences found in demersal deep-sea fish assemblages between the Mediterranean and the Atlantic reinforces not only the general view of the Mediterranean deep-sea as an oligotrophic ecosystem (e.g. Bouchet and Taviani, 1992), but also the view that there are distinct differences in the size-related structure of the fish populations. The primary cause of the differences in size structure is probably a result of adaptations at both the species and ecosystem level to different trophic relationships between the two areas. The historical evolution of the Mediterranean basin, its geomorphology and markedly different environmental conditions and fishing pattern must also contribute to the differences.

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APPENDIX. – Fish species captured in the four studied areas (BB, Balearic basin; AB, Algerian basin; RT, Rockall Trough; PS, Porcupine Seabight), with their bathymetric range (m) and frequency of occurrence (%) within this depth interval.

Family	Species	BB Depth	%	AB Depth	%	RT Depth	%	PS Depth	%
Myxinidae	*Myxine ios*							985-1650	33
Hexanchidae	*Hexanchus griseus*	986-1045	43					960	-
Scyliorhinidae	*Apristurus* sp.					962-1750	81	1024-1448	11
	Galeus melastomus	429-1739	71	402-1713	79	530-582	100	506-848	18
	Galeus murinus					962-1235	42	1024	-
	Scyliorhinus canicula			402	-				
	Scymnodon ringens					530-775	43	706-982	44
Squalidae	*Centrophorus squamosus*					775-962	50	986	-
	Centrophorus uyato			802	-				
	Centroscyllium fabricii					1032-1545	60		
	Centroscymnus coelolepis	1419-1862	58	1012-1713	57	962-1750	54	1027-1720	30
	Centroscymnus crepidater					880-1197	72		
	Dalatias licha	984-1794	13	595-891	40	530-772	33	545-1360	10
	Deania calceus					582-1032	38	740	-
	Etmopterus princeps					962-1805	43	1533-1720	29
	Etmopterus spinax	429-1488	45	415-1416	82	530	-	407-1790	14
Rajidae	*Bathyraja richardsoni*							1987	-
	Breviraja caerulea					1197-1205	100	1390	-
	Raja naevus			908	-				
	Raja (*Dipturus*) *nidarosiensis*					962-1235	26	1263-1312	40
	Raja (*Leucoraja*) *circularis*							695	-
	Raja (*Rajella*) *bathyphila*					1450-1870	20		
	Raja (*Rajella*) *bigelowi*					1717-1750	100	1845-1987	60
	Raja (*Rajella*) *fyllae*					972-1197	62	1024	-
Chimaeridae	*Chimaera monstrosa*	1225	-		-	530-1545	94	470-1742	38
	Hydrolagus affinis					1715-1870	50	1720-1993	20
	Hydrolagus mirabilis					742-1235	100	695-1452	52
	Hydrolagus pallidus					1717	-		
Rhinochimaeridae	*Rhinochimaera atlantica*[1]					1205	-	1360-1533	40
Alepocephalidae	*Alepocephalus agassizii*					1717-1955	67	1650-1993	44
	Alepocephalus australis					1485	-	1587-1789	37
	Alepocephalus bairdii					742-1805	88	706-1900	42
	Alepocephalus productus							1533-1987	30
	Alepocephalus rostratus	615-1862	100	699-1713	90	962-1235	47	706-1452	56
	Bathytroctes microlepis							1845-1975	56
	Conocara macroptera					1485	-	1527-1932	83
	Conocara murrayi					1955	-	1440-1993	41
	Narcetes stomias							1867-1900	50
	Photostylus pycnopterus							1390	
	Rouleina attrita					1545-1870	43	1312-1927	50
	Xenodermichthys copei					582-1870	53	577-1975	59
Searsiidae	*Holtbyrnia anomala*					1717	-		
	Normichthys operosus					1470-1545	67		
Photichthyidae	*Polymetme corythaeola*							472-706	27
Argentinidae	*Argentina silus*					530-582	100	407-695	75
Synodontidae	*Bathysaurus ferox*					1870	-	1587-1987	53
Chlorophthalmidae	*Bathypterois dubius*					1197-1545	43	986-1900	83
	Bathypterois mediterraneus	931-1862	93	908-1713	100				
	Chlorophthalmus agassizii			402-601	43				
Notosudidae	*Scopelosaurus lepidus*							750-1867	10
Nettastomatidae	*Nettastoma melanurum*	651-1078	71	415-1416	71				
	Venefica proboscidea							1527	-
Congridae	*Conger conger*	831	-	693-816	67	530	-		
Derichthyidae	*Nessorhamphus ingolfianus*							1205	-
Synaphobranchidae	*Dysomma brevirostre*	498-615	60	601	-				
	Histiobranchus bathybius							1790-1975	20
	Ilyophis arx							1789-1900	29
	Ilyophis blachei					1192-1235	50	1284-1789	40
	Ilyophis brunneus							1533-1884	43
	Synaphobranchus kaupi					530-1955	100	407-1993	99
Haulosauridae	*Aldrovandia* sp.					985	-		
	Halosauropsis macrochir					1717-1955	83	1440-1993	78
	Halosaurus johnsonianus					1032-1205	40	1379-1448	75
Notacanthidae	*Notacanthus bonapartei*	498-1862	72	595-1513	54	530-1955	79	470-1975	76
	Notacanthus chemnitzii					572-1235	26	763-1390	30
	Polyacanthonotus challengeri							1742-1987	15
	Polyacanthonotus rissoanus	710-1862	94	693-1709	38	747-1955	91	740-1993	76
Macrouridae	*Coelorhynchus abditilux*							848-1024	22
	Coelorinchus coelorhincus	532	-	402-415	100	530-772	83	407-1312	23
	Coelorhynchus labiatus	1049-1844	67	1012-1713	90	747-1870	94	472-1900	46

APPENDIX (Cont.). – Fish species captured in the four studied areas (BB, Balearic basin; AB, Algerian basin; RT, Rockall Trough; PS, Porcupine Seabight), with their bathymetric range (m) and frequency of occurrence (%) within this depth interval.

Family	Species	BB Depth	%	AB Depth	%	RT Depth	%	PS Depth	%
	Coryphaenoides (C.) brevibarbis					1750-1955	60	1845-1993	27
	Coryphaenoides (C.) leptolepis							1993	-
	Coryphaenoides (C.) mediterraneus	970-1862	52	1094-1713	83	1032-1955	76	1272-1993	82
	Coryphaenoides (L.) carapinus							1742-1975	17
	Coryphaenoides (C.) guentheri	1308-1862	93	1417-1713	33	962-1955	73	1263-1993	94
	Coryphaenoides (C.) rupestris					530-1870	100	706-1932	72
	Hymenocephalus italicus	429-831	100	402-898	100			472	-
	Malacocephalus laevis					572-582	100	407-512	71
	Nezumia aequalis	532-1212	96	502-1407	100	572-1205	92	472-1650	66
	Trachyrhynchus murrayi					962-1545	74	1205-1600	95
	Trachyrhynchhus scabrus	429-1589	73	601-816	62			506-1360	49
Gadidae	*Brosme brosme*					530-992	19		
	Gadiculus argenteus			402-601	43	530-775	57	407-793	32
	Antonogadus macrophthalmus					530-1197	31	407-1263	26
	Antonogadus megalokynodon	429-1212	70	402-802	83				
	Merluccius merluccius	710-1075	11	402-802	50	572	-	506-785	29
	Micromesistius poutassou	429-556	60	402-816	43	530-1955	23	407-804	38
	Molva dypterygia dypterygia					530-1470	77	490-1257	10
	Molva dypterygia macrophthalma			402	-			470-695	27
	Molva molva					530	-		
	Onogadus argentatus							1024	-
	Phycis blennoides	429-1308	88	402-1032	100	530-1012	59	407-1027	73
	Phycis phycis								
Moridae	*Antimora rostrata*					1192-1955	87	982-1993	52
	Eretmophorus kleinenbergi	931	-						
	Halargyreus johnsonii					572-1235	78	545-1900	57
	Laemonema latifrons							985-1867	11
	Lepidion eques					530-1235	100	506-1524	96
	Lepidion guentheri	1584-1862	44	1591-1713	60				
	Lepidion lepidion	651-1862	100	908-1713	86				
	Mora moro	532-1589	77	693-1305	89	530-1007	71	500-1312	70
	Rhynchogadus hepaticus	429	-						
Berycidae	*Beryx decadactylus*							506	-
Trachichthyidae	*Hoplostethus atlanticus*					1032-1235	83	960-1677	65
	Hoplostethus mediterraneus	764	-	502-1322	60			527-848	95
Oreosomatidae	*Neocyttus helgae*							1024	-
Apogonidae	*Epigonus denticulatus*	429-1008	29	402-813	46				
	Epigonus telescopus	970	-	802-816	67	530-992	56	490-1027	50
Trichiuridae	*Aphanopus carbo*					530-1205	52	1025-1993	10
	Lepidopus caudatus			402-601	71				
Callionymidae	*Synchiropus phaeton*			402-543	40				
Zoarcidae	*Lycodes atlanticus*							1217-1742	33
	Lycodes crassiceps							1506-1975	14
	Melanostigma atlanticum	532-1409	61			880-1235	65	763-1506	12
Bythitidae	*Cataetyx alleni*	532-1851	91	699-1622	26			1205	-
	Cataetyx laticeps	1739-1862	42	1713	-	1470-1805	75	1440-1993	52
Ophidiidae	*Benthocometes robustus*	458-532	67						
	Spectrunculus grandis					1750-1955	80	1742-1993	71
Aphyonidae	*Sciadonus galatheae*							1789	-
Carapidae	*Echiodon drummondi*							407-545	56
	Echiodon dentatus	429	-						
Scorpaenidae	*Helicolenus dactylopterus*	429-751	55	402-543	100	530-880	67	407-848	67
	Scorpaena elongata			402	-				
	Sebastes viviparus					582	-		
	Trachyscorpia cristulata echinata							763-1036	72
Triglidae	*Trigla lyra*			402	-				
Peristediidae	*Peristedion cataphractum*			402	-				
Psychrolutidae	*Cottunculus thomsonii*					962-1545	39	1016-1448	45
Liparididae	*Paraliparis caudani*					747-1197	27	695-1016	54
	Paraliparis leptochirus	615-764	83	601-1233	42				
Scophthalmidae	*Lepidorhombus boscii*	429-984	17	415-595	60	530-875	50	407-785	23
	Lepidorhombus whiffiagonis					530-582	100	407-545	44
Pleuronectidae	*Glyptocephalus cynoglossus*					530-1197	23	407-506	50
Soleidae	*Bathysolea profundicola*							527	-
	Microchirus variegatus							506	-
Cynoglossidae	*Symphurus ligulatus*	532-1049	70	415-898	87				
	Symphurus nigrescens	429-615	100	402-601	71				
Lophiidae	*Lophius piscatorius*	429-1008	10			742-1032	55	407-793	36
	Lophius budegassa			402	-				

[1] For taxonomic composition analysis, this species has been included within the family Chimaeridae.